THE SENSORY BASIS OF HOST RECOGNITION BY SYMBIOTIC SHRIMPS, GENUS *BETAEUS* [1]

BARRY W. ACHE [2] AND DEMOREST DAVENPORT

*Department of Biological Sciences, University of California,
Santa Barbara, California 93106*

Animals living in symbioses serve as excellent material for the analysis of external stimuli controlling adaptive behavior. To a mobile partner, the host organism represents a principal source of environmental stimuli, a source easily manipulated by the investigator. Experimental analyses of symbiotic relationships have demonstrated that chemical substances of host origin elicit host-oriented behavior in crustacean species associated with pelecypods (Sastry and Menzel, 1962), polychaetes (Carton, 1968; Davenport, Camougis and Hickok, 1960), echinoids (Gray, McClosky and Wiehe, 1968), and amphinurans (Webster, 1968). These studies focused primarily on the role of chemical stimuli in effecting the respective symbiotic relationships. In surveying earlier work on crustacean orientation, however, Pardi and Papi (1961) note that even such relatively simple behavioral responses as kinetic and tactic orientation appear to be governed by higher neural centers, sometimes utilizing information from multiple sensory modalities. More recently, the interaction of multi-modal stimuli has been demonstrated to elicit and direct feeding behavior in several species of decapod crustaceans (Hiatt, 1948; Symons, 1964; Hazlett, 1968).

The carideans *Betaeus harfordi* (Kingsley) and *Betaeus macginiticae* Hart are two of five species of betaeid shrimps adapted to a symbiotic existence (Hart, 1964). *Betaeus harfordi* occurs in the mantle cavity of all eight species of California abalone, *Haliotis* spp. (Cox, 1962; Hart, 1964). *B. macginiticae* associates predominantly with the homochromous giant red sea urchin, *Strongylocentrotus franciscanus* (Agassiz) and occasionally with the purple urchin, *S. purpuratus* (Simpson) (Ache, 1970; Hart, 1964). Laboratory observations indicate that adult shrimps of both species leave their hosts during dark periods and return directly from distances up to 1 m away within a few minutes of the onset of light. (Ache, 1970). In doing so, they provide a behavioral response, *i.e.*, tactic locomotion toward the host, suitable for analysis of the stimuli mediating distant host recognition.

The present investigation attempts to elucidate and compare the sensory bases of the host location behavior of *B. harfordi* and *B. macginiticae* and to explain the apparent specificity of their respective relationships in terms of the sensory competence of the shrimps.

[2] Present address: Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33432.

Organisms

Specimens of *Betaeus harfordi* and *B. macginiticae,* 1.0–3.5 cm total length, were collected along with their respective hosts, the abalones, *Haliotis corrugata* Gray, *H. rufescens* Swainson, and *H. cracherodii* Leach and the urchin, *Strongylocentrotus franciscanus,* from subtidal populations in the Santa Barbara area. Shrimps were maintained in the laboratory isolated from their hosts on a diet of frozen *Artemia*. Shrimps were utilized for experimentation between the 2nd and 10th days of holding. Hosts or other organisms to be tested as potential sources of stimuli (test organisms) were held without feeding and utilized within three days of laboratory confinement.

Apparatus

Two types of choice apparatus were utilized to quantify the host-oriented behavior of *Betaeus*. One apparatus was simply a large (1.0 × 1.3 × 0.2 m) seawater-filled rectangular tank or arena. Seawater was continuously introduced via four inlet tubes, one located in each corner of the tank, and maintained at a
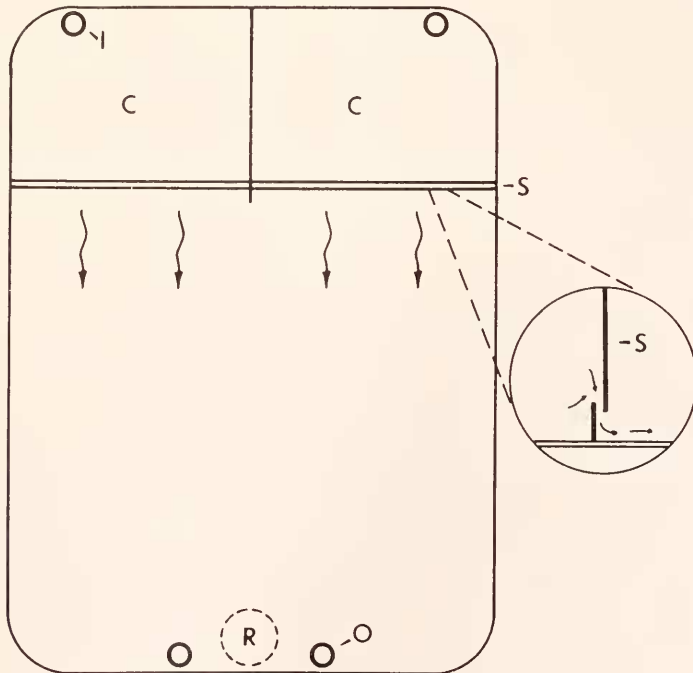

FIGURE 1. Diagram (top view) of two-celled choice apparatus: C—test or control cells; I—seawater inlets; O—seawater outlets; S—transparent plexiglass screen; R—removable release cylinder. Arrows indicate direction of flow into choice area. Inset is transverse view of continuous opening along bottom of plexiglass screen. Arrows indicate flow through this opening.

depth of 15 cm by two clear plastic standpipe drains centered on the longer axis
of the tank. Plastic-coated screens fitted into each of the corners served to con-
fine test organisms within approximately 15 cm of the seawater inlets, yet did not
retard the movement of shrimps into or out of the corner compartments. A remov-
able length of 14 cm diameter clear plastic tubing centered in the tank served as a
release point for shrimps. The overhead fluorescent lamps of the room supplied
relatively uniform illumination to the apparatus.

Shrimp behavior was also quantified in a 2-celled choice apparatus designed
to be compatible with the fast-moving *Betaeus* yet retain the binomial simplicity
of a conventional Y maze. The apparatus (Fig. 1) incorporated a $33 \times 46 \times 12$ cm
opaque white polyethylene pan fitted with a T-shaped transparent plastic divider
to form two small compartments (herein referred to as test and control cells)
and a larger compartment (herein referred to as the choice area). A baffled
opening in the transverse partition (inset, Fig. 1) allowed seawater introduced
into the test and control cells to flow into the choice area where it was removed
by two constant-level siphons. An input of 7.0 ml/sec of new seawater to each
cell produced an even, laminar flow of approximately 5 mm/sec along the bottom
of the choice area (arrows, Fig. 1). A removable opaque cylinder allowed intro-
duction of single shrimp into the choice area with minimal directional bias. A 7.5w
frosted incandescent lamp centered over the apparatus 50 cm from the water's sur-
face supplied even, low-intensity illumination to the choice area. The 2-celled
choice apparatus was adapted for detailed analysis of visual stimuli by replacing
the open-bottomed transparent partition with a watertight transparent partition to
insure chemical isolation of all three compartments and by removing the seawater
inlet and outlet tubes to create a static system. A 4 cm strip of opaque white
plastic attached to the transparent panel to increase the separation between the
two cells enhanced the resolution of right and left choices.

Procedure and data analysis

Shrimps were isolated from their hosts up to 10 days prior to testing. Symons
(1964) has noted that the ability of either chemical or tactile stimuli to evoke feed-
ing in the crab *Hemigrapsus oregonensis* increases over a 10 day period of starva-
tion, approaching the ability of combined tactile-chemical stimuli to elicit the same
response by day 10. To minimize any bias due to threshold change, all our
experiments within a series were performed in as short a time as possible.

Arena apparatus—Ten minutes prior to introduction of the shrimps two to
four host organisms were placed in each of two diagonally opposite corner com-
partments. As controls, three non-host organisms, the seastar *Dermasterias
imbricata,* were placed in each of the two remaining corner compartments. The
presence of other live organisms in the control compartments minimized the
possibility of the data reflecting a generalized response to any animate object.
The animal complement of each compartment was equated by weight ($\pm$ 50 g) to
the mean weight of three seastars, 320 g. Twelve or 15 shrimp selected from
a group of 120–125 individuals were dip-netted into the central release cylinder,
held for 5 minutes, and then released by removing the cylinder. The location of
each individual was recorded 30 minutes following release. This sequence was
repeated eight times for any one set of test conditions, with the contents of the

corner compartments moved clockwise one compartment with each repetition. Mucus and debris were wiped from each compartment with each rotation.

The hypothesis that the terminal distribution of shrimp was randomly divided between the two pair of corner compartments was tested by comparing the total number of shrimps found within the two host-containing compartments with the number found within the two control compartments. In each experiment, the probability of obtaining the observed distribution was tested for its association with a theoretical distribution of 0.50–0.50, utilizing chi-square.

Two-celled choice apparatus.—Experimental protocol with this apparatus consisted of introducing potential sources of stimuli to one or both of the cells, allowing 10 minutes for equilibration, and monitoring the time ($t \lessgtr 6$ min) required for each of 30 shrimps, individually and sequentially introduced, to leave the release point, traverse the length of the choice area, and contact the transparent partition delimiting one of the two cells. Thirty shrimps, selected at random from groups of 70–80 individuals, were utilized in each experiment. Experiments comprising an experimental series utilized the same group of 70–80 shrimps. A new group of 70–80 shrimps was obtained for each experimental series. The contents of the two cells were exchanged in each experiment after testing one-half of the 30 shrimps, the exchange being accompanied by washing and refilling of the apparatus with fresh seawater. Data displaying a significant non-experimental bias ($P < 0.05$) to either cell were voided and the experiment repeated. This practice, which required repetition of approximately 8% of the experiments, effectively controlled for transient bias (*e.g.*, obstruction of an inlet tube by particulate material) that may have occurred during the course of an experiment.

The number of shrimps reaching criterion, *i.e.*, those contacting the transparent partition delimiting the host-containing cell, was compared by chi-square analysis to an expected distribution in which 50% of the total number of individuals making a choice go to each cell. This value is subsequently referred to as "χ^2 choice." In many experiments, a number of individuals failed to move, or move but failed to reach criterion within the 6 minute experimental period. For an experiment questioning the relative attractiveness of a stimulus situation, the number of organisms not reaching criterion represents significant information. Formulation of this category involves combining the number of individuals not moving, those moving but not reaching criterion, and those choosing the control cell. Although detailed *a priori* knowledge of how shrimps making a choice relate to those not stimulated to move remains unknown, individuals of all three combined groups can be considered as not displaying a positive response to the stimulus source of a particular experiment. This rationale is not without precedent (see Davenport, 1950). Differences in the numbers of shrimps failing to reach criterion for any two experiments of a series were tested for significance with a two-way contingency analysis adjusted for continuity. (Simpson, Roe, and Lewontin, 1960, page 190).

RESULTS

The Betaeus-Haliotis *association*

Experiments utilizing arena apparatus. These experiments attend to the question: Do shrimps collected from the host, *H. rufescens*, require both chemical and

Arena experiments: B. harfordi-H. rufescens vs. D. imbricata

Experiment	Stimulus modality removed	Shrimps tested	Shrimps choosing		x^2 choice	P
			Host	Control		
1	None	96	82	8	72.3	<0.005
2	Chemical	111	29	38	0.12	0.50–0.75
3	Visual	111	78	25	27.2	<0.005
4	None, hosts in all corners	96	34	48	2.38	0.10–0.25

visual stimuli of host origin to effect host location?   Shrimps were permitted to choose between two corner compartments containing host abalone and two containing the control organism while visual or chemical stimuli were selectively removed from the choice situation.   Table I summarizes the results of these experiments which extended over an eight day period.   With both visual and chemical stimuli present, shrimps preferentially selected those compartments containing abalone, *H. rufescens*, over those containing the seastars (Experiment 1). With all organisms contained in clear glass 4 liter beakers to eliminate chemical stimuli from the choice situation, but otherwise identical protocol maintained, the differential response elicited in Experiment 1 was abolished (Experiment 2). However, with the corner compartments covered with eight layers of white cheesecloth so as to exclude visual stimuli from the choice situation yet not alter the flow characteristics of the system, shrimps exhibited preferential selection of the abalone-containing compartments (Experiment 3).   To further eliminate the possibility that bias existed in the experimental procedure itself, host abalones were substituted for seastars in the control compartments, *i.e.,* all compartments contained host abalone, and Experiment 1 was repeated (Experiment 4).   No significant difference occurred in the number of shrimps selecting either of the two pair of host-containing compartments.

Testing shrimps in groups introduced the possibility of bias due to shrimp-shrimp interactions.   The 30 minute experimental period allowed multiple responses by any one shrimp, which were observed to occur in a small percentage of the trials.   For these reasons, and since more than 50% of the shrimps entered a corner compartment within the first 3–4 minutes of the 30 minute experimental period, further analysis utilized the 2-celled choice appartus, designed for short term observation of individual organisms.

Experiments utilizing 2-celled choice apparatus.   The question considered in the preceding group of experiments was again tested as a basis for comparison of the two techniques.   In these experiments, shrimps collected from the abalone, *H. corrugata*, were permitted to choose between: Experiment 1—a test cell containing seawater only, Experiment 2—as Experiment 1 only with the transverse partition covered with an opaque screen to remove visual stimuli from the choice situation, Experiment 3—as Experiment 1 only with the abalone contained in a clear glass 4-liter beaker to remove chemical stimuli from the choice situation and Experiment 4—two control cells containing seawater only.   Table II (Series 1) summarizes the results of these experiments.   Significantly different choice be-

tween test and control cells was elicited only in the presence of chemical stimuli of host origin. Essentially the same number of shrimps located the host-containing cell when only chemical stimuli were present (Experiment 2) as when both visual and chemical were present, *e.g.*, the experimentally unaltered situation (Experiment 1).

To gain a fuller understanding of the results of Series 1 experiments, it was necessary to know if the presence of chemical stimuli triggered a response to current, since chemical stimuli were always presented in association with a directional flow of water emanating from the test and control cells. Table II (Series 2) summarizes the results of experiments designed to answer this question.

Shrimps in Series 2 experiments were collected from the host abalone, *H. rufescens*. Experiment 1 represents the experimentally unaltered choice situation. To determine if current alone had any effect, shrimps were permitted to discriminate between a test cell containing the model abalone and a seawater control cell both with (Experiment 2) and without (Experiment 3) a current in the apparatus. To eliminate current, the seawater inlets were closed. Substituting a model abalone for a live one in the test cell allowed presentation of visual stimuli without chemical stimuli while retaining the directional flow. The model consisted of a paraffin-filled abalone shell with 1.5 cm wide "epipodium" of black tape exposed beneath the ventral edge of the shell. As live abalone remained stationary when placed in the apparatus, a static model was judged an acceptable substitute. As can be seen, differential choice between test and control cells was not elicited in either experiment. Likewise, a test of association comparing the number of shrimps choosing the model-containing cell *vs.* the number not choosing it between the two experiments indicates no difference in the response of the shrimps $\chi^2 -$ 0.223, $P - 0.50$–0.75). It appears that current itself does not effect the activity of the shrimps nor their response to visual stimuli.

To determine if the presence of non-directional chemical stimuli had any effect, shrimps were permitted to discriminate between test and control cells when non-directional chemical stimuli of host origin were present throughout the system, but in the absence of a flow (Experiment 4). Two specimens of *H. rufescens* (350 g), confined in a perforated plastic cup and swirled in the choice area of the apparatus for 1 minute prior to introduction of each shrimp, served to introduce non-directional chemical stimuli into the system. Assuming host effluents had an effective time stability of at least 6.0 minutes, host effluent was present in the choice area throughout the maximum time interval allowed for choice. This assumption, of course, could only be confirmed by a positive result, *i.e.*, by obtaining a significant change in response on the addition of such non-directional chemical stimuli. Differential choice was elicited in favor of the model-containing cell, suggesting that the presence of non-directional chemical stimuli may enhance the stimulus value of visual cues characterizing the model host. A test of association comparing the number of shrimps choosing the model-containing cell *vs.* the number not choosing it in this (Experiment 4) and in the control situation (Experiment 3—no current, no chemical), however, indicates that no significant increase in the level of activity occurred in the presence of the non-directional chemical stimuli ($\chi^2 - 0.178$, $P - 0.50$–0.75). It appears that non-directional

chemical stimuli alone are not sufficient to affect the activity of the shrimps, although they may enhance directed activity in the presence of visual cues.

To determine if non-directional chemical stimuli serve to trigger a response to current, shrimps were permitted to discriminate between test and control cells when non-directional chemical stimuli of host origin were presented simultaneously with a directional flow (Experiment 5). No differential choice was elicited between the test and control cells. However, the method of introducing the chemical stimuli in this experiment should have dispersed host effluent throughout all compartments of the apparatus. Since a current was flowing under the transparent partition from both test and control cells, no difference should have existed in the stimulus pattern characterizing the two cells except for the visual stimuli of the model-containing cell. Experiments 2 and 3 indicate that visual stimuli with or without current elicit little activity. Thus, the combined number of shrimps reaching either cell can be considered as being most characteristic of the response to this stimulus situation. A test of association comparing the total number of shrimps choosing either cell $vs.$ the number not choosing either cell in Experiment 5 and in the basic host response (Experiment 1—visual, current, and directed chemical stimuli of host origin), indicates no significant difference in the level of activity ($P > 0.995$). Host-oriented locomotion in the shrimp $B.$ $harfordi$ appears

TABLE II

Two-celled choice experiments: B. harfordi

Experiment	Contents of test cell	Stimulus modalities present*	Shrimps choosing		χ^2 Choice	P
			Test	Control		
Series 1						
1	$H.$ $corrugata$	V, DC	26	1	23.0	<0.005
2	$H.$ $corrugata$	DC	25	2	19.6	<0.005
3	$H.$ $corrugata$	V	14	6	1.60	0.10–0.25
4	Seawater	—	4	4	—	—
Series 2						
1	$H.$ $rufescens$	V, DC, C	26	0	26.0	<0.005
2	$H.$ $rufescens$	V, C	2	2	—	—
3	$H.$ $rufescens$	V	4	3	0.14	0.50–0.75
4	$H.$ $ryfescens$	V, NDC	8	0	8.00	<0.005
5	$H.$ $rufescens$	V, NDC, C	14	10	0.67	0.25–0.50
Series 3						
1	$H.$ $cracherodii$	DC	25	0	25.0	<0.005
2	Seawater	—	5	2	1.29	0.25–0.50
3	$H.$ $rufescens$	DC	24	0	24.0	<0.005
4	$H.$ $corrugata$	DC	28	0	28.0	<0.005
5	$K.$ $kelletia$	DC	8	8	—	—
6	$S.$ $franciscanus$	DC	9	4	1.92	0.10–0.25
7	$M.$ $crenulata$	DC	6	8	0.28	0.50–0.75
8	$U.$ $caupo$	DC	7	2	2.78	0.05–0.10
9	$H.$ $cracherodii$	DC	27	1	24.2	<0.005
10	Seawater	—	4	7	0.81	0.25–0.50

* V, visual; DC, directed chemical; NDC, non-directed chemical; C, current.

to result from the ability of chemical stimuli to release a response to directional water currents in these shrimp.

It was then asked: Is the distribution of the active substance(s) sufficiently restricted to explain the apparent specificity of association of the shrimps to molluscs of the genus *Haliotis?* Table II (Series 3) summarizes experiments extending over five consecutive days that permitted specimens of *B. harfordi* collected from the abalone, *H. cracherodii,* to discriminate between a test cell containing individuals of one of seven different species of test organisms and a control cell containing only seawater. An opaque white plastic screen placed over the transverse partition occluded visual stimuli from the choice situation. Test organism complements were equated to 350 ± 50 g wet weight. Significantly different choice was elicited by effluents of test organisms of the genus *Haliotis* (Experiments 1, 3, 4, 9). Differential choice was not elicited by effluents of two other gastropods, the neogastropod *Kelettia kelletii* (Experiment 5) and the archeogastropod *Megathura crenulata* (Experiment 7). Similarly, differential choice was not elicited by effluents of the echiuroid *Urechis caupo* (Experiment 8) nor of the echinoid *Strongylocentrotus franciscanus* (Experiment 6), both reported to be hosts of congeneric *Betaeus* species (Hart, 1964). Agreement of initial and terminal replicates of the basic host response (Experiments 1, 9) suggests the lack of response in the latter experiments was not the result of a temporal change in responsiveness of the shrimps.

The total number of shrimps locating tests cells containing *Haliotis* spp. was greater than for the non haliotid species. A test of association on the results of the most and least extreme distributions obtained with *Haliotis* effluents (Experiments 3, 4) indicates no significant difference between the numbers of shrimps locating the test cell in these experiments ($\chi^2 - 0.935$, $P - 0.25$–0.50). A test of association on the results of the least extreme distribution obtained with a *Haliotis* effluent (Experiment 3) and the least extreme distribution obtained with non-host effluent (Experiment 6), however, indicated a significant difference between the number of shrimps locating the test cells ($\chi^2 - 22.9$, $P - < 0.005$). It follows that the remaining and more extreme distributions obtained to non-host effluents are also significantly different from the distribution obtained in Experiment 3.

The Betaeus-Strongylocentrotus *association*

Experiments utilizing arena apparatus. The question was first asked whether shrimps in association with the urchin *S. franciscanus* require both chemical and

TABLE III

Arena experiments: B. macginitieae — S. franciscanus vs. D. imbricata

Experiment	Stimulus modality removed	Shrimps tested	Shrimps choosing		χ^2 choice	P
			Host	Control		
1	None	111	89	13	56.6	<0.005
2	Chemical	111	63	25	15.4	<0.005
3	Visual	96	63	12	35.4	<0.005
4	None, hosts in all corners	99	44	47	0.09	0.75–0.90

visual stimuli of host origin to effect host location. Shrimps were permitted to make a choice when presented with two corner compartments containing host urchins and two containing the control organism. Visual or chemical stimuli were then selectively removed from the choice situation. Table III summarizes the results of these experiments which extended over a period of 8 days. Experiment 1 represents the basic host-location response of shrimps in the arena apparatus when neither chemical nor visual stimuli were altered, *i.e.*, the "natural" stimulus condition. A significantly greater number of shrimps selected the two host-containing cells. When both the test and control organisms were contained in clear glass 4-liter beakers to eliminate chemical stimuli from the choice situation and an otherwise identical experimental protocol maintained (Experiment 2), significantly more shrimps still selected the host-containing compartments. Likewise, with the corner compartments covered with eight layers of white cheesecloth so as to exclude visual stimuli yet not alter the flow characteristics of the system and retain chemical stimuli (Experiment 3), significantly more shrimps selected the host-containing compartments. Experiment 4, in which host sea urchins were substituted for the seastars in the control compartments (*i.e.*, all compartments contained host urchins) suggests that final distributions of this series of experiments were not biased by the experimental procedure itself.

Experiments utilizing 2-celled choice apparatus. For the reasons previously described, more detailed analyses utilized the 2-celled choice apparatus. Repetition of the above described experiments provided a basis for comparison of the two techniques of behavioral quantification. Table IV (Series 1) summarizes the results of these experiments. Shrimps were permitted to select between a test cell containing the host urchin and a control cell containing seawater only. In the basic stimulus situation, where both chemical and visual stimuli were experimentally unaltered, significantly more shrimps selected the host-containing cell (Experiment 1). With the host urchin contained in a clear glass 4-liter beaker placed in the test cell and a seawater filled beaker placed in the control cell, significantly more shrimps still selected the host-containing cell (Experiment 2). With an opaque white plastic screen attached to the transverse partition thus masking visual stimuli from the choice situation while not interfering with chemical stimuli, significantly more shrimps again selected the host-containing cell (Experiment 3). Neither stimulus modality acting alone, however, elicited host location to the extent that both did when presented together. Very few shrimps made a choice in the absence of any stimuli of host origin (Experiment 4). These data are in agreement with those of the arena experiments indicating that either chemical or visual stimuli of host origin are sufficient to effect host location by these shrimps.

The question was then asked to what extent can the response to chemical stimuli explain the apparent specificity of the *B. macginiticae-Strongylocentrotus* association. Screening the transparent plexiglass divider with a thin sheet of opaque white plastic arranged so as not to alter the flow characteristics of the apparatus effectively blocked visual communication between the cells and the choice area, while allowing free passage of chemical cues. The mean weight of the test organisms utilized in each experiment was 200 ± 25 g. In a series of experiments extending over five consecutive days, shrimps were permitted to

Experiment	Contents of test cell	Stimulus modalities present*	Shrimps choosing		χ^2 Choice	P
			Test	Control		
Series 1						
1	S. franciscanus	V, C	28	1	25.0	<0.005
2	S. franciscanus	V	22	0	22.0	<0.005
3	S. franciscanus	C	22	1	19.2	<0.005
4	Seawater	—	2	2	—	
Series 2						
1	S. franciscanus	C	25	0	25.0	<0.005
2	Seawater	—	4	2	0.66	0.25–0.50
3	S. purpuratus	C	20	0	20.0	<0.005
4	L. anamesus	C	5	1	2.66	0.10–0.25
5	S. parvimensis	C	8	6	0.57	0.25–0.50
6	D. imbricata	C	8	6	0.57	0.25–0.50
7	H. rufescens	C	9	6	0.60	0.25–0.50
8	U. caupo	C	8	5	0.69	0.25–0.50
9	S. franciscanus	C	21	1	18.2	<0.005
10	Seawater	—	3	5	0.50	0.50–0.75

* V, visual; C, chemical; —, neither visual or chemical.

discriminate between a test cell containing one of seven different species of test organism and a control cell containing seawater only (Table IV, Series 2). Only effluent of the congeneric echinoids, *S. franciscanus*, the natural host (Experiments 1, 9), and *S. purpuratus*, (Experiment 3), elicited differential choice between test and control cells. Differential choice was not elicited by effluents of the non-host echinoid, *Lytechinus anamesus* (Experiment 4), nor the non-echinoid echinoderms, *Stichopus parvimensis* (Experiment 5) and *Dermasterias imbricata* (Experiment 6). Likewise, effluents of the abalone, *Haliotis rufescens* (Experiment 7), and the echiurid worm, *Urechis caupo*, (Experiment 8) both reported hosts for congeneric *Betaeus* species (Hart, 1964), failed to elicit differential choice. A test of association indicates that the final distribution elicited by effluents of the urchin, *S. purpuratus* (Experiment 3), does not differ significantly from the more extreme of the two distributions elicited by effluents of the natural host (Experiment 1) ($\chi^2 = 1.46$, $P = 0.1$–0.25). That the distribution elicited by non-strongyloid effluents differs significantly from that obtained in Experiments 1, 3, and 9, is indicated by a test of association of the least extreme distribution obtained with *S. franciscanus* effluent (Experiment 9) and the least extreme distribution obtained with a non-host effluent, that of the abalone, *H. rufescens* (Experiment 7) ($\chi^2 = 13.3$, $P = $ < 0.005). Only a few individuals responded in the absence of any stimuli of host origin (Experiments 2, 10). Agreement of initial and final repetitions of the basic host response (Experiments 1, 9) support the hypothesis that no change occurred in the response level of the shrimps during the duration of the experimenal period.

The question was then asked to what extent can the response to visual stimuli of host origin explain the apparent specificity of the *B. macginitieae-Stronglyocentrotus* association. These experiments utilized the static modification of the 2-celled

choice apparatus in which chemical stimuli and the carrier flow are absent from the choice situation. As a preliminary experiment, shrimps were permitted to select between a cell containing the host *S. franciscanus* and a cell containing one of five different test organisms, the host, *S. franciscanus,* the abalone, *Haliotis rufescens,* the holothuroid, *Stichopus parvimensis,* the alternate host, *Strongylocentrotus purpuratus,* and the giant keyhole limpet, *Megathura crenulata.* These animals represent the predominant, non-sessile, macrobenthic fauna of the Santa Barbara collection site. All test organisms were equated for displacement volume (+ 50 ml). Shrimps selected the host-containing cell in all cases except in the pairing of the limpet, *Megathura,* and the host urchin. These experiments were not pursued further, however, due to the difficulty in equating such diverse organisms for "unit" characteristics.

As an alternative approach to gaining an understanding of the visual basis of the shrimp-urchin association, an effort was made to determine which component(s) of the total visual pattern characterizing *S. franciscanus* is (are) utilized by the shrimps to effect visually-mediated host recognition. These experiments quantified the ability of shrimps to visually distinguish between two simultaneously presented objects (Cell A and Cell B). Any shrimp not moving away from the release point by 5.5 minutes was touched on the telson with a camel's hair brush, which served as sufficient stimulus to initiate movement to criterion in

TABLE V

B. macginitieae: *analysis of stimulus parameters visually characterizing* Strongylocentrotus franciscanus

Experiment	Cell A	Shrimps choosing A	Shrimps choosing B	Cell B	χ^2 choice	P
1	Urchin (9.0)*	23	7	Urchin (6.4)	8.52	<0.005
	Urchin (6.4)	21	9	Urchin (4.5)	4.80	0.025–0.05
2	Spineless urchin (8.0)	18	12	Intact urchin (4.0)	1.20	0.25–0.50
3	Disk (10.0)	14	16	Urchin (7.5)	1.34	0.75–0.90
	Disk (10.0)	18	12	Urchin (5.0)	1.20	0.25–0.50
	Disk (10.0)	28	2	Urchin (3.5)	22.4	<0.005
4	Disk (9.0)	27	3	Patterned disk (9.0)	19.2	<0.005
5	Black disk, white bkgd. (3.8)	24	5	White disk, black bkgd. (3.8)	12.5	<0.005
6	Disk (9.0)	20	9	Serrated disk (9.0)	4.16	0.025–0.05
	Disk (9.0)	17	13	Square (7.9)**	0.53	0.25–0.50
	Disk (9.0)	7	23	Square (8.9)	19.2	<0.005
	Disk (6.0)	15	14	Square (5.3)	0.03	0.75–0.90
	Disk (9.0)	14	15	Triangle (12.5)	0.03	0.75–0.90
	Disk (9.0)	15	13	Inverted triangle (12.5)	0.14	0.50–0.75

* No. indicates maximum test diameter or diameter of disk model, cm.
** No. indicates length of single side of model, cm.

most shrimps within the 6.0 minute test period. Table V summarizes the results of these investigations.

To determine whether urchins are discriminated by size, shrimps were permitted to choose between a moderate and a larger-sized urchin, as well as between the same moderate-sized urchin and a smaller one (Experiment 1). In each case, the cell containing the larger urchin of the pair was favored. To test the possibility that larger shrimps preferentially choose larger urchins, a two-way contingency analysis was applied to the number of small (< 1.5 cm total length) and large (> 2.5 cm total length) shrimps choosing the larger of the two hosts in each pairing. Moderate sized shrimps were not included in this calculation in order to produce more discrete size classes of small and large individuals. For both pairings, the hypothesis of no difference in response between small and large sized shrimps could not be rejected ($\chi^2 = 1.82, 1.56; P = 0.10–0.25$).

To determine if urchins are recognized by the presence of spines, shrimps were permitted to choose between a large urchin (8.0 cm test diameter) from which all spines had been clipped off to within 0.5 cm of the test and a small urchin (4.0 cm test diameter) from which only the tips of the longest spines had been clipped to obtain a peripheral diameter of 9.0 cm (Experiment 2). Both "urchins" had the same peripheral diameter thus minimizing experimental bias due to a size difference between the two test objects. If the presence of spines or the spinose form was an attractive parameter, shrimps should favor the smaller of the two urchins, i.e., the one with spines essentially intact. Neither cell was favored, however. If spines are not necessary for urchin recognition, it should further be possible to construct a solid dark colored model that could not be differentiated from an intact urchin of equal effective visual diameter. Two-dimensional models fashioned from thin sheet plastic and painted flat black were presented by mounting them on a panel of clear plastic centered vertically in the test cell. Since it was not possible a priori to equate disk diameter with urchin peripheral diameter, a series of three pairings was conducted in which shrimps were permitted to choose between a 10 cm diameter black disk and one of three different sized urchins (Experiment 3). No discrimination was obtained in favor of either cell when intact urchins of 7.5 and 5.0 cm test diameter were paired with the disk. With a more extreme size differential, a 10 cm disk vs. a 3.5 cm test diameter urchin, however, the cell containing the solid disk was favored.

A third experiment was directed towards evaluating spines as a parameter of recognition. Shrimps were permitted to choose between a 9.0 cm diameter solid black disk and a 9.0 cm diameter patterned black-white disk consisting of a "checker-board" of alternating black and white squares 1.0 cm on a side (Experiment 4). If shrimps recognize the spinose form of the urchin on the basis of the internal contrast, the patterned black-white disk, with its greater internal contrast, should be favored over the solid disk of equal peripheral diameter. The cell containing the solid disk was favored over that containing the patterned disk.

To determine if urchins are differentiated as a discrete form per se or as a contrasting pattern with the background, the transparent "windows" of the test cells were masked with opaque screens. The size of a disk was calculated so that its total area equaled one-half the area of the opaque screens and a disk centered on each screen. Shrimps were permitted to distinguish between a white disk

presented against a black background and black disk presented against a white background (Experiment 5). Both models contain equal areas of black and white. Both contain equal zones of black-white boundary. Both models should be equally attractive if shrimps are responding to the amount of light-dark contrast. The cell containing the black disk against the white background was favored over the reverse combination.

To determine if urchins are differentiated on the basis of their peripheral outline, shrimps were permitted to choose between a 9.0 cm diameter disk and a series of two dimensional shapes (Experiment 6). A 9.0 cm diameter solid black disk was favored over a 9.0 cm diameter serrated black disk with 28 equally-spaced serrations cut radially to a depth of 2.0 cm. Neither cell was favored on presentation of a solid, black square, 7.9 cm on a side, and a 9.0 cm diameter solid disk, these models enclosing equal areas. However, if the size of the square shape was increased so that its area equaled 1.3 times that of the 9.0 cm diameter disk (*i.e.*, 8.9 cm per side), the shrimps favored the cell containing the square shape. To control the possibility that the overall size of the models exceeded the visual angle subtended by the shrimps' eyes, the square-disk pairing was again presented except that the area was reduced and equated to that of a 6.0 cm diameter disk (square 5.3 cm per side). As with the larger models, neither cell was favored in this latter pairing. Finally, shrimps did not discriminate between 9.0 cm diameter solid black disk and a solid black equilateral triangle of equal area (12.5 cm per side), either with the triangle oriented point upward or inverted with the point downward. Experiment 6 supports the conclusion that visual recognition of the host urchin, *S. franciscanus*, by the shrimps is not based on the perception of the urchin as a round or circular form.

DISCUSSION

The data support the hypothesis that *B. harfordi* is able to effect distant host recognition utilizing chemical stimuli of host origin alone. It is not suggested that visual cues are entirely without effect when available. Indeed, Experiments 1–3 and 2–4 (Table II) suggest that visual stimuli of host origin may elicit a low response under certain conditions. However, both these apparent responses to visual stimuli can also be explained as a generalized response toward the only contrasting object in an otherwise monotonous choice situation. The results of Experiment 2–2 (Table II) which incorporate essentially the same stimulus parameters as Experiment 1–3 (Table II) did not indicate any tendency of the shrimp to select the model-containing cell. It is interesting to note that subtidal species of *Haliotis* are frequently heavily encrusted with epiphytic growths and contrast little with the surrounding substrate (Cox, 1962). However, the black epipodium of at least one of the subtidal species, *H. rufescens*, could offer sufficient contrast with the background to facilitate visual recognition at close range.

A question arises as to the ability of chemical stimuli alone to effect directed locomotion towards an odor source (Fraenkel and Gunn, 1961; Gage, 1966). In the marine benthos local water turbulence and surging would disrupt diffusion gradients required for chemotaxic orientation. It appears that *B. harfordi* can utilize the directional component of a carrier current containing host factor to

effect host location by moving "upstream" in the presence of the appropriate chemical releaser. This mechanism reportedly occurs in other crustaceans (Allee, 1916; Luther, 1930), although to the authors' knowledge it has not been investigated in any detail. Laverack (1962) has demonstrated low frequency tactile receptors in *Homarus* chelae, sensitive to water currents down to 0.3 cm/sec. Low threshold chemoreceptors have been well documented in the crustacea (*e.g.*, review of Laverack, 1968). Such a mechanism would be adaptive in that it would not require chemoreceptor competence sufficient to discriminate the very small increments in chemical concentration required for chemotaxic orientation, but merely the presence or absence of the attractant.

Specificity experiments suggest that *B. harfordi* discriminates a chemical substance or complex of substances containing sufficient information for recognizing gastropods of the genus *Haliotis* from other gastropods and from the non-molluscan hosts of other betaeid shrimps. The data do not eliminate the possibility that this chemically-mediated genus-specific recognition is based on quantitative rather than qualitative differences in the attractants. The fact that equal masses of test organisms were contained directly in a continuously flowing seawater wash minimizes experimentally induced variations in stimulus concentration, so even quantitative differences in the same attractant must be considered as potentially significant mechanism for maintenance of this association. Recently, evidence has been presented that quantitative odor differences are at least partially responsible for mediating escape/attack behavior in a marine gastropod (Snyder and Snyder, 1971).

Previous investigations indicate a relative high degree of chemosensory competence in crustaceans. Symbiotic pinnotherids, *Pinnixa chaetopterana*, discriminate effluents of host polychaetes of the genera *Chaetopterus* and *Amphritrite* from those of the non-host polychaete genera, *Nereis* and *Arenicola* (Davenport *et al.*, 1960). Another symbiotic pinnotherid, *Dissodactylus mellitae*, discriminates its host echinoid, *Mellita quinquiesperforata*, from six other species of echinoderms, although it reportedly can be conditioned to respond to another flattened echinoid, *Encope mitchelini* (Gray *et al.*, 1968). More specific discrimination has been reported (Carton, 1968) for the parasitic copepod *Sabelliphilus sarsi* which can discriminate by chemical means between its host polychaete, *Spirographis spallanzani* and two non-host but congeneric polychaetes, *S. pavonina* and *S. spallanzani* var. *brevispira*. By nature of their action, crustacean sex phermones (Atema and Engstrom, 1971; Kittredge, Terry and Takahashi, 1971; Ryan, 1966) could also be considered species-specific chemical attractants, but the possibility that other stimulus modalities confer the species specificity to crustacean chemically-mediated mate recognition remains to be disproven.

B. macginitieae, in contrast to *B. harfordi*, appears to use both visually and chemically mediated information for distant host recognition. The interaction of chemical and current stimuli was not adequately investigated for *B. macginitieae*, and thus is not reported here. Visually mediated information would contain sufficient directionality, however, to allow directed locomotion in situations offering both chemical and visual stimuli, even in the absence of current flow. It is possible that chemical and visual cues, acting together enhance the value of the stimulus situation to the shrimps. More shrimps located the host urchins in the arena

experiment presenting both stimuli simultaneously than in those lacking either visual or chemical cues (Table III, Experiments 1, 2, 3). Such apparent enchancement does not necessarily result from neural summation of the sensory information contained in the two stimulus modalities, however, since it could also be explained by chemically released hyperactivity increasing the probability that visually directed locomotion towards the host occurs within the test period. The data do not allow resolution of this question, but the phenomenon is worthy of further investigation. Symons (1964) earlier reported that the number of feeding movements nearly doubled in the crab *Hemigrapsus oregonensis* when elicited by both chemical and tactile stimuli together than by either stimulus modality operating alone.

The specificity of the *Betaeus-Strongylocentrotus* association in nature is somewhat unclear. Hart (1964) described the species with nine specimens, one pair collected from *S. purpuratus,* one female from *S. franciscanus,* and six with no host record. In an area abundant with both urchin species, over 1000 specimens of *B. macginiticae* were collected, associated in all but one instance with specimens of *S. franciscanus.* This fact, along with the fact that *B. macginiticae* is homochromous with *S. franciscanus* and behaviorally adapted to move among the long spines of this urchin (Ache, 1970) suggests that *S. franciscanus* may be the "preferred" host of *B. macginiticae* and *S. purpuratus* a secondary host.

Chemical stimuli contain sufficient information to allow the urchin symbionts to discriminate urchins of the genus *Strongylocentrotus* from other echinoderms and from the non-echinoderm hosts of other betaeid shrimps, a level of sensory competence at least functionally similar to that of *B. harfordi.* Visually mediated information is sufficient to allow *B. macginiticae* to further discriminate between the two reported strongylocentrotid hosts. The long-spined, brick red (occasionally to light red) *S. franciscanus* is morphologically distinct from the short-spined, smaller, light purple *S. purpuratus* (Ricketts and Calvin, 1968). Thus *B. macginiticae* with its demonstrated ability to visually discriminate large, dark "solid" objects could differentiate between the two urchin species. Visually-mediated behavior is not commonly reported to occur in aquatic crustaceans, although its role is rather well documented in the control of sexual and agonistic behavior of semi-terrestrial species (*e.g.,* reviews of Schone, 1968; Salmon and Atsaides, 1968; Wright, 1968). Alverdes (1930) noted that the aquatic branchyuran *Carcinus maenas* and the anomuran *Eupagurus bernhardus* confronted by two black screens will move between them, but before doing so beat their antennae in the direction of each of the screens, behavior he interpreted as suggesting that perception of the screen as objects does occur. Visually-mediated food location behavior has been reported for the aquatic anomuran *Clibanarius vittatus* (Hazelett, 1968) and the intertidal brachyuran *Pachygrapsus crassipes* (Hiatt, 1948) although these latter observations were conducted on crabs in air. Symons (1964) was unable to demonstrate either a releasing or directing effect of visually-mediated stimuli on the feeding behavior of the aquatic brachyuran *Hemigrapsus oregonensis.*

Question arises as to the ability of visual stimuli acting alone to effect a response specific to *S. franciscanus* if *B. macginiticae* is not responding to any visual parameter uniquely characteristic of its host. Experiments showed that the predominately black hemispherical *Megathura* was not distinguished from the host *S. franciscanus* in a paired choice situation, although visual stimuli proved

sufficient for discrimination of the host urchin from other lighter-pigmented organisms. The possibility must be considered that few other large, dark-pigmented organisms like *Megathura* may occur in the subtidal rocky habitat of the range ascribed by Hart for the *Betaeus-Strongylocentrotus* association (Santa Catalina Island, Monterey, California). Further experimentation, however, is necessary to clarify this point.

A visual receptor capable of rudimentary form vision would be sufficient to effect the visually-mediated behavior demonstrated by the shrimps. As noted by Carthy (1958), what appears to be simple form recognition of dark shapes can frequently be explained by the alternative hypothesis of a negative phototaxis towards a zone of reduced light intensity. That a more complex response than simple negative phototaxis is involved is demonstrated by the preference of *B. macginiticae* for the black circle presented against a white background over the white circle presented against a black background (Table V, Experiment 5). Both models presented equal zones of contrast and equal areas of reduced intensity. This is not to imply that the shrimps are not negatively phototactic; it has been shown they are (Ache, 1970). The peripheral outline of the model does not appear to be an active parameter in discrimination (Table V, Experiment 6) suggesting that the attractive factor may be more the "solidness" of the form than its specific shape—*e.g.*, circular or semi-elliptical as the urchin test. The preference of shrimps for the solid circle over the black-white checkerboard-patterned model (Table V, Experiment 4) also supports this idea.

The possibility of color discrimination has not been eliminated by these experiments. Two factors tend to discredit the possibility that *S. franciscanus* is recognized on the basis of color. Black models proved as equally attractive as naturally pigmented urchins, when equated for effective visual diameter (Table V, Experiment 3). Also the extinction coefficients of coastal seawaters are greater for longer wavelengths of visible light required for color discrimination of a red pigmented organism (for coastal water off Southern California-Young and Gordon, 1939). However, Wald and Seldin (1968) have demonstrated differential sensitivity of two components of the ERG in the shrimp *Palaemontes vulgaris* which they suggest may represent the red- and violet-sensitive components of a visual mechanism for color differentiation. The results of the present experiments, however, indicate that intensity discrimination would be sufficient to explain the visually-mediated component of host recognition.

It appears then that information from several sensory modalities is utilized by both *B. harfordi* and *B. macginiticae* to effect their respective symbiotic relationships. This mechanism serves to reduce the demands on the competence of any one receptor type, while maximizing the discriminating ability of the shrimps both in regards to stimulus directionality (the *B. harfordi* studies) and stimulus specificity (the *B. macginiticae* studies). The present experiments do not allow resolution of whether the action of such multi-modal information is simply additive or involves summation and perhaps additional integration in higher neural centers. Certainly, centers of higher order neural integration receiving visual information and input from other sensory modalities, including chemosensory information, are known to exist in the eyestalks of *Panulirus argus* (Maynard and Dingle, 1963; Maynard and Yager, 1968) and probably in other decapod species

(Hazlett, 1971). Work towards resloving this question is currently in progress using crustaceans of several species.

Summary

1. The sensory basis of host-oriented locomotion in the caridean *Betaeus macginiticae* contrasts with that of the congeneric *B. harfordi*. Both of these shrimps can locate their respective host organisms utilizing chemical stimuli of host origin. Only *B. macginiticae* demonstrates the ability to utilize visual stimuli for this same purpose.

2. By using information contained in multiple stimulus modalities, *B. macginiticae* is able to maintain a more restricted host association than its congener.

3. Visual recognition of its urchin host by *B. macginiticae* does not involve any parameter of the total visual pattern of the urchin that uniquely characterizes the urchin species, but appears to be a generalized response to larger, dark forms of undefined peripheral outline.

4. Positive rheotaxis in the presence of appropriate non-directional chemical stimuli is suggested as the mechanism by which *B. harfordi* effects chemically-mediated host location.

LITERATURE CITED

ACHE, B. W., 1970. An analysis of the sensory basis of host recognition in symbiotic shrimp of the Genus *Betaeus*. *Ph.D. thesis, University of California*, Santa Barbara, 120 pp.

ALLEE, W. C., 1916. Chemical control of rheotaxis in *Ascellus*. *J. Exp. Zool*, **21** : 163–198.

ALVERDES, F., 1930. Tierpsychologische Analyse der intracentralen Vorange welche bei decapoden Krebsen die locomotrischen Reaktionen auf Helligkeit und Dunkelheit bestimmen. *Z. Wiss. Zool.*, **137** : 403–475.

ATEMA, J., AND D. ENGSTROM, 1971. Sex phermone in the lobster, *Homarus americanus*. *Nature*, **232** : 261–263.

CARTHY, J. D., 1958. *An Introduction to the Behavior of Invertebrates*. Hafner, New York, 380 pp.

CARTON, Y., 1968. Specificite parasitaire de *Sabelliphilus sarsi,* parasite de *Spriographis spallanzani.* III. Mise en evidence d'une attraction biochemique du copepode par l'Annelide. *Arch. Zool. Exp. Gen.,* **109** : 123–144.

COX, K. W., 1962. California abalones, Family Haliotidae. *Calif. Dept. Fish Game, Fish Bull.,* **118** : 1–133.

DAVENPORT, D., 1950. Studies in the physiology of commensalism. I. The polynoid genus *Arctonoe. Biol. Bull.,* **98** : 81–93.

DAVENPORT, D., G. CAMOUGIS AND J. F. HICKOK, 1960. Analyses of the behavior of commensals in host-factor. 1. A hesioned polychaete and a pinnotherid crab. *Anim. Behav.*, **8** : 209–218.

FRAENKEL, G. S., AND D. L. GUNN, 1961. *The Orientation of Animals.* [2nd Edition] Dover Publications, New York, 376 pp.

GAGE, J., 1966. Experiments with the behavior of the bivalves, *Montacuta substriata* and *M. ferruginosa,* 'commensals' with spatangoids. *J. Mar. Biol. Ass. U. K.,* **46** : 71–88.

GRAY, I. E., L. R. McCLOSKY AND S. C. WIEHE, 1968. The commensal crab, *Dissodactylus mellitae,* and its reaction to sand dollar host-factor. *J. Elisha Mitchell Sci. Soc.,* **84** : 472–481.

HART, J. F. L., 1964. Shrimps of the genus *Betaeus* on the Pacific coast of North America with descriptions of three new species. *Proc. U. S. Nat. Mus.,* **115** : 431–466.

HAZLETT, B. A., 1968. Stimuli involved in the feeding behavior of the hermit crab, *Clibanarius vittatus* (Decapoda, Paguridae). *Crustaceana,* **15** : 305–311.

HAZLETT, B. A., 1971. Non-visual functions of crustacean eyestalk ganglia. *Z. Vergl. Physiol.,* **71** : 1–13.

HIATT, R. W., 1948. The biology of the lined shore crab, *Pachgrapsus crassipes* Randall. *Pac. Sci.,* **2**: 135–213.

KITTREDGE, J. S., M TERRY AND F. T. TAKAHASI, 1971. Sex pheromone activity of the molting hormone, crustecdysone, on male crabs. *Fishery Bulletin,* **69**: 337–343.

LAVERACK, M. S., 1962. Responses of cuticular sense organs of the lobster, *Homarus vulgaris* (Crustacea) 1. Hair-peg organs as water current receptors. *Comp. Biochem. Physiol.,* **5**: 319–325.

LAVERACK, M. S., 1968. On the receptors of marine invertebrates. Pages 249–324 in H. Barnes, Ed., *Animal Review of Oceanography and Marine Biology,* Vol. 6. Allen and Unwin, London.

LUTHER, W., 1930. Versuche über die chemorezeption der Brachyuren. *Z. Vergl. Physiol.,* **12**: 117–205.

MAYNARD, D. M., AND H. DINGLE, 1963. An effect of eyestalk ablation on antennular function in the spiny lobster *Panulirus argus. Z. Vergl. Physiol.,* **46**: 515–540.

MAYNARD, D. M., AND J. G. YAGER, 1968. Function of an eyestalk ganglion, the *medulla terminalis,* in olfactory integration in the lobster, *Panulirus argus. Z. Vergl. Physiol.,* **59**: 241–249.

PARDI, L., AND F. PAPI, 1961. Kinetic and tactic responses. Pages 385 in T. H. Waterman, Ed., *The Physiology of Crustacea II.* Academic Press, New York.

RICKETTS, E. F., AND J. CALVIN, 1969. *Between Pacific Tides.* [4th Edition] Stanford Univ., Press, Palo Alto, 614 pp.

RYAN, E. P., 1966. Pheromone: evidence in a decapod crustacean. *Science,* **151**: 340–341.

SALMON, M., AND J. P. ATSAIDES, 1968. Visual and acoustical signalling during courtship by fiddler crabs (Genus *Uca*). *Amer. Zool.,* **8**: 623–639.

SASTRY, A. N., AND R. W. MENZEL, 1962. Influence of hosts on the behavior of the commensal crab, *Pinnotheres maculatus* Say. *Biol. Bull.,* **123**: 388–395.

SCHÖNE, H., 1968. Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. *Amer. Zool.,* **8**: 641–654.

SIMPSON, G. G., A. ROE AND R. C. LEWONTIN, 1960. *Qantitative Zoology.* [Rev. Edition] Harcourt, Brace and Co., New York, 440 pp.

SNYDER, N. F. R., AND H. A. SNYDER, 1971. Pheromone-mediated behavior of *Fasciolaria tulipa. Anim. Behav.,* **19**: 257–268.

SYMONS, P. E. K., 1964. Behavioral responses of the crab *Hemigrapsus oregonensis* to temperture, diurnal light variation and food stimuli. *Ecology,* **45**: 580–591.

WALD, G., AND E. B. SELDIN, 1968. Spectral sensitivity of the common prawn, *Palaemonetes vulgaris. J. Gen. Physiol.,* **51**: 694–700.

WEBSTER, S. K., 1968. An investigation of the commensals of *Cryptochiton stelleri* in the Monterey Penninsula area, California. *Veliger,* **11**: 121–125.

WRIGHT, H. O., 1968. Visual displays in brachyuran crabs: Field and laboratory studies. *Amer. Zool.,* **8**: 655–665.

YOUNG, R. T., JR., AND R. D. GORDON, 1939. Report on the penetration of light into the Pacific Ocean off the coast of Southern California. *Scripps Inst. Oceangr. Univ. Calif. Bull., Tech. Ser.,* **4**: 197–218.